EDAPHIC CONTROL OF VEGETATIONAL PATTERN IN EAST COAST FORESTS.

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(Five Text-figures.)

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Synopsis.

This study attempts to place in exploratory perspective some of the edaphic factors responsible for the complex vegetational pattern in east coast forests. Relationships between forest communities characterized by the presence of blackbutt (*Eucalyptus pilularis* Sm.) and white mahogany (*E. acmenioides, E. umbra*), and the relationship of each to rainforest have been examined, and the following tentative conclusions reached:

(i) Distribution of blackbutt is limited by physical properties of the soil which restrict aeration, moisture permeability or penetration of roots to depth; these soil properties vary with the mineralogical composition of the parent material, its geological history, and the landscape pattern.

(ii) Narrow ranges of available moisture associated with some rainforest soils suggest that where other factors are not limiting, soil moisture availability could be a critical factor in distribution of rainforest in east coast forests.

(iii) Soil fertility status is not a determining factor in the delimitation of blackbutt and white mahogany communities, but within each community a gradient of increasing soil fertility is largely responsible for the vegetational gradient from dry sclerophyll forest to rainforest; along this fertility gradient the vegetation, and particularly the occurrence of rainforest, may be restricted by limiting physical properties of the soil and the soil moisture availability.

(iv) The influence of eucalypts on their own sites may be a factor contributing to the marked sensitivity of eucalypt communities to minor habitat variations.

The eucalypt-rainforest relationship is discussed in terms of the concept that both the sclerophyllous dominants and the rainforest element stratum change sensitively and predictably along environmental gradients.

Introduction.

The coastal forests of south-eastern Australia may be characterized by a mosaic of eucalypt species associations and a complex relationship of eucalypt sclerophyll and rainforest (Fig. 1). There have been a number of ecological studies in these forests (Fraser and Vickery, 1937, 38, 39; Pidgeon, 1942; Burges and Johnston, 1953), but until more recent years (Beadle, 1954, 62; Webb, 1956, 59; Baur, 1957) there has been little emphasis on the analysis of vegetation-environment relationships.

This current study is complementary to an analysis of vegetation pattern in east coast forests (Florence, 1963), and attempts to place in exploratory perspective some of the environmental factors responsible for the vegetational mosaic.

I. The Vegetation Pattern.

Partly because of their obvious complexity, there has been little attention directed towards an understanding of eucalypt species and species association relationships. A given species, for example, may exhibit an apparent sensitivity to minor habitat variation within any one situation, but nevertheless it may occur over wide geographic and habitat ranges. Development of concepts concerning ecological-genetic relationships within *Eucalyptus* (Pryor, 1953, 1959) has provided some initial perspective of species relationships; these concepts include (i) that *Eucalyptus* may be subdivided into four principal groups (subgenera) which are reproductively isolated from one another; (ii) that interbreeding eucalypt species occupy distinctly different ecological situations;

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(iii) that many reproductively isolated eucalypt species occur together in pairs which are ecologically co-extensive for a major portion of their ranges, though usually separated at the extremes.

With the exception of blackbutt (*Eucalyptus pilularis* Sm.) the pattern of distribution of members of the interbreeding group Renantherae in east coast forests would be in substantial agreement with the principle that interbreeding species occupy distinctly different habitats. Distribution of blackbutt is best illustrated as one superimposed on the distinctive habitat situations of each of the other Renantherae and,

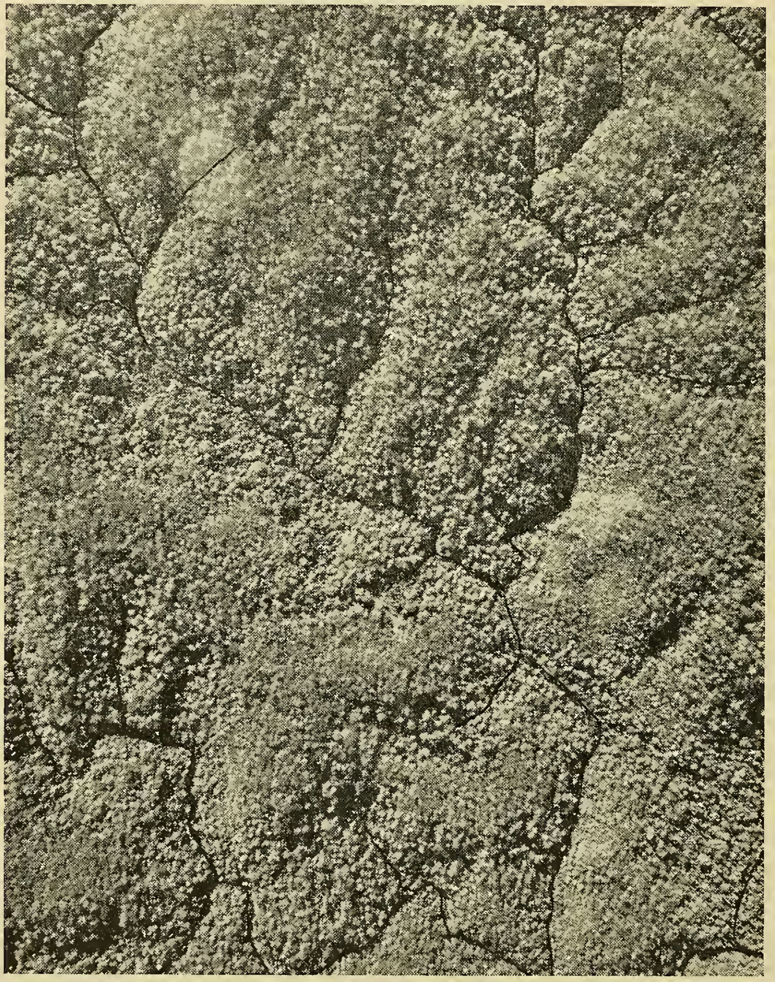

Fig. 1.—Air Photo.

Fig. 1. Complex vegetational pattern on part of Mount Boss State Forest No. 910; scale averages slightly more than 20 chains to inch. Symbols are: *Rm,* rainforest characterized by presence of *Ceratopetalum*; *Ry,* rainforest characterized by presence of *Argyrodendron*; *Rs,* depauperate rainforest, *Myrtus* sp. usually dominant; *Mb, Tristania conferta, Syncarpia glomulifera, E. microcorys, E. saligna* dominating a well-developed rainforest element stratum; *Mm, E. microcorys, E. saligna* dominant with *T. conferta, S. glomulifera, E. acmenioides* and rainforest element associated; *Bp, E. pilularis* dominant with *E. microcorys, E. saligna, E. gummifera* associated, some rainforest element; *Bh, E. acmenioides, E. microcorys, E. gummifera, E. pilularis*; *Dm, E. umbra, E. globoidea, E. tereticornis,* little or no rainforest element; *Cr,* rock outcrops.

Acknowledgement is made to the Forestry Commission of New South Wales for provision of the Air Photo, and for the interpretation of the vegetational pattern.

although they are largely separate, there may be a considerable degree of cohabitation of interbreeding species within each situation (Florence, 1963).

In this study, environmental relationships between forest communities characterized by the presence of blackbutt and white mahogany (*E. acmenioides* Schau., or *E. umbra**), both members of the Renantherae, and the relationship of each to rainforest are examined. Throughout their common range (Fig. 2), blackbutt and white mahogany communities are often sharply delineated, but alternatively, in other situations there may be a wide co-occurrence. Within its community blackbutt reaches

Fig. 1.—Vegetational Pattern.

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* Blake (*Proc. Roy. Soc. Qld.*, 69: 86) synonymized *E. umbra* R. T. Bak. and *E. carnea* R. T. Bak. in 1958, and in this and the previous paper relating to vegetational pattern in east coast forests (Florence, 1963), the terminology *E. umbra* has been used in Blake's sense. However, Johnson (*Contrib. N.S.W. Nat. Herbarium*, 3: 103) has subsequently recognized two subspecies, *E. umbra* ssp. *umbra* and *E. umbra* ssp. *carnea*. Along the vegetational gradient from rainforest to the more depauperate dry sclerophyll, *E. umbra* ssp. *carnea* might be regarded as ecologically intermediate between *E. acmenioides* and *E. umbra* ssp. *umbra*. For the most part, *E. umbra* referred to in this and the preceding paper is *E. umbra* ssp. *carnea*, although much intermediacy between the two ssp. was observed.

very high levels of ecological "importance", and may in fact be the only dominant present. From this situation blackbutt's vegetational gradient may be regarded as moving in two directions, towards dry sclerophyll forest and towards rainforest. Along the latter gradient a characteristic assemblage of rainforest element species may form a secondary stratum to the dominants—blackbutt, Sydney blue gum (*E. saligna* Sm.), tallowwood (*E. microcorys* F.v.M.), turpentine (*Syncarpia glomulifera* Sm.—Niedenzu), brush box (*Tristania conferta* R.Br.), and others. Nevertheless along this vegetational gradient towards rainforest, the upper limit of blackbutt's environmental tolerance is apparently well short of that necessary for rainforest[1] formation, so that a mixed sclerophyll-rainforest element community without blackbutt is frequently interposed between blackbutt forest and rainforest.

White mahogany occupies a total vegetational gradient largely parallel to that of blackbutt, but in contrast to blackbutt, *E. acmenioides* will occur in situations directly marginal to rainforest. Along the white mahogany gradient from rainforest to dry sclerophyll forest, *E. umbra* is considered to replace *E. acmenioides* in the more open sclerophyllous situations and the gradient continue to quite depauperate dry sclerophyll.

II. The Climatic Environment.

Vegetational and environmental studies were carried out within the coastal region extending from Batemans Bay to Fraser Island (Fig. 2). In this zone the climate is characterized by a predominantly summer rainfall, a mean monthly rainfall less than 200 points for no more than one month of the year and the Australian maxima for rainfall "effectiveness" and "reliability" (Leeper, 1949). An adaptation from Swain's Climatic Index for Australia (de Beuzeville, 1943) illustrates the essential climatic data for this zone (Fig. 3). In view of the probable influence of more or less annual and sometimes extended spring and summer droughts on the Australian vegetation, Swain's Index is based on the continuity or otherwise of rainfall throughout the year, and has mean annual rainfall (MAR) as a subordinate factor. Other factors included in the Index are the mean temperature of the coldest month (MTCM) and the temperature range as expressed by the mean temperature of the hottest month (MTHM) in relation to (MTCM). The index defines with some precision the geographic limits of the vegetation studied. For example, the blackbutt range is entirely associated with the coastal zone demarcated by the numeral "1". North of Fraser Island the zone with initial numeral "3" has increasing duration of drought, and just beyond the southern extremity of the coastline illustrated, zone "1" is replaced by zone "2", indicating the change from summer to winter dominant rainfall.

Within the coastal zone of optimum rainfall and rainfall uniformity in Australia, variation in MAR from as low as 40″ and up to 100″ per annum is related largely to elevation and distance from the coast of the sinuous mountain system that extends along the whole of Australia's east coast. For example, the increasing drought in zone "3" north of Gympie (Qld.) is related in part to the westward swing of this mountain system. Although elevation, through its effect on rainfall and temperature, has an apparent influence on vegetation, it is nevertheless clear that macroclimatic factors cannot explain the often sharp discontinuities in blackbutt, white mahogany and rainforest distribution that characterize much of their common range.

III. The Geological Factor in the Vegetation Pattern.

While the geological mosaic along the east coast of New South Wales and southern Queensland is clearly responsible for some major features of the vegetational pattern, the parent material-vegetation relationship is by no means a simple one, particularly in respect to the nature and distribution of rainforests.

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[1] In this paper, the term "rainforest" refers specifically to a closed community forming a deep densely interlacing canopy, and from which a sclerophyllous overstorey is absent; species occurring in mixture with sclerophyll dominants are referred to as a "rainforest element".

Delineation of Blackbutt and White Mahogany.

Although blackbutt extends from the New South Wales/Victorian border to Fraser Island in Queensland its most continuous and extensive occurrences are in the middle of its range and associated with (1) the Lorne Triassic Basin (north of Taree) and (2) Silurian schists and shales (Coffs Harbour District).

Sedimentary depositions within the Lorne Basin include basal beds of massive conglomerate, ferruginous grits, sandstones, shales and soft clay shales. The vegetational structure of the blackbutt forest may be correlated with gradation in depositions; conglomerates and coarse sandstone-derived soils support blackbutt communities characteristic of its vegetational gradient towards dry sclerophyll forest, red-brown finer sandstones support near optimum blackbutt stands, and fine sandstones and shales support stands characteristic of the vegetational gradient towards rainforest.

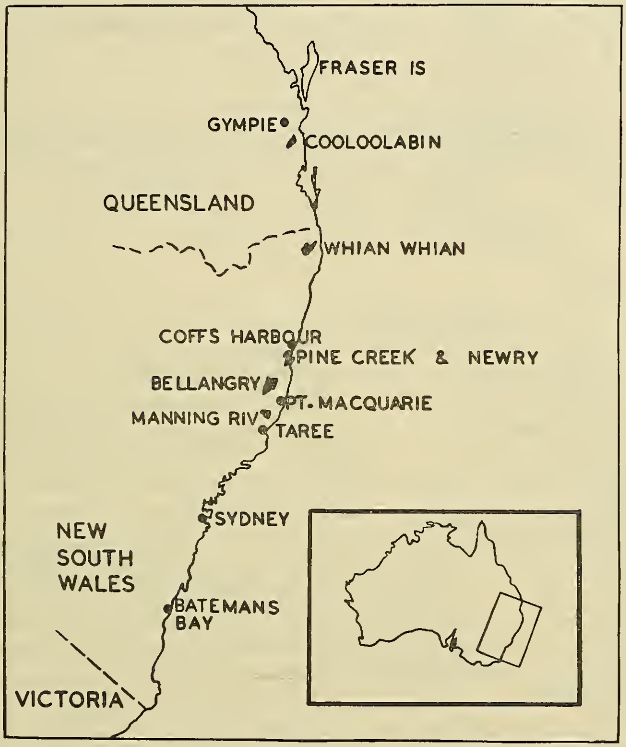


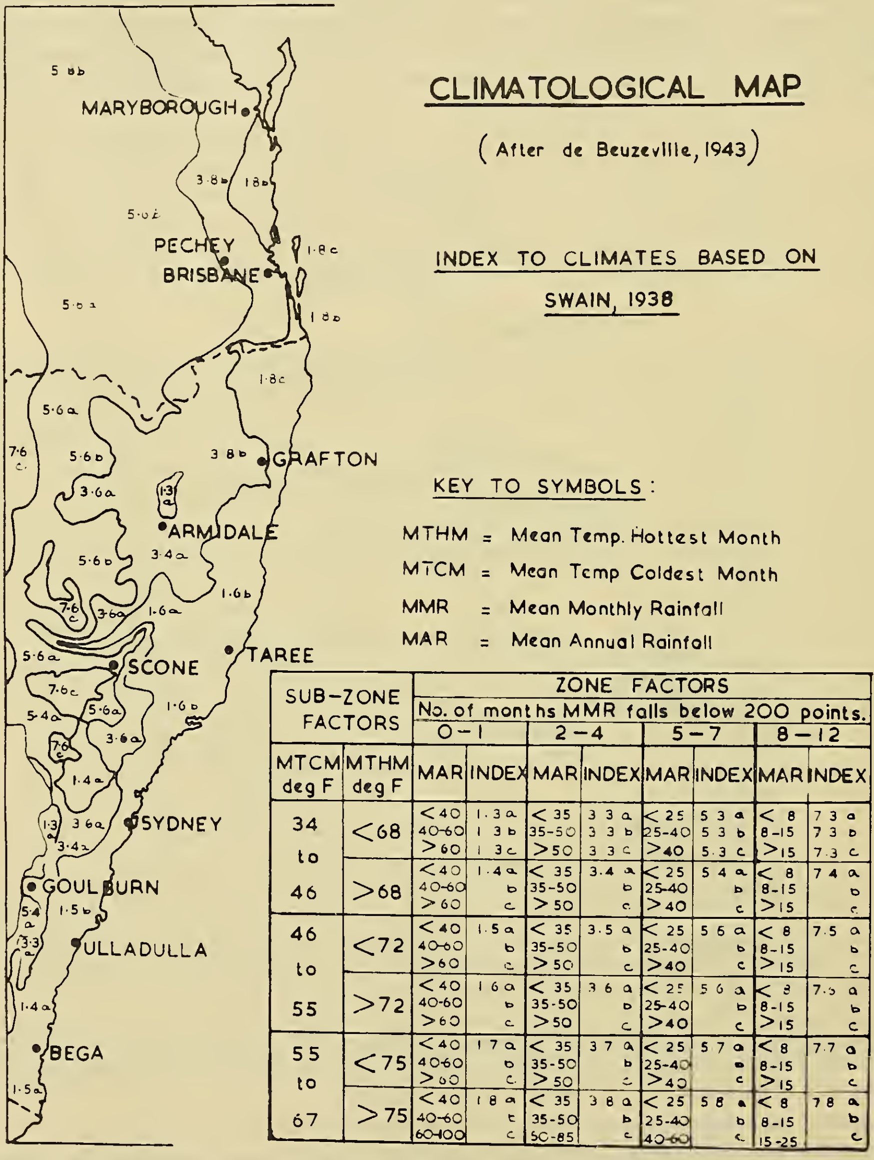
Fig. 2. Part of the east coast of southern Australia showing place names referred to in text.

Blackbutt (*Eucalyptus pilularis*) has a distribution from the Victoria-New South Wales border to Fraser Island, and the common range of blackbutt and white mahogany (*E. acmenioides, E. umbra*) extends from about Sydney to Fraser Is.

Within the Lorne Basin discontinuity in blackbutt distribution is correlated with outcrops of the underlying Carboniferous formation, with "alkaline intrusives" (Voisey, 1939), and with fine felspathic sandstone and siltstone.

On the mid-north coast of New South Wales blackbutt has a relatively continuous distribution on the extensive schist and shale soils. On the schist soil of Pine Creek and Newry State Forests, discontinuity of blackbutt and white mahogany forest is associated with variation in the bedding of the rock and in the consequent nature of the rock-soil relationship. Apart from this differentiation, the alignment of blackbutt forest on ridges, rainforest in gullies, and with white mahogany forest interposed, is common through a large part of this formation. This pattern has presented one of the most complex problems in understanding the environmental relationships involved (Section VII).

Together, the Permian and Carboniferous formations provide one of the major barriers to a more widespread occurrence of blackbutt forest. A great diversity of vegetation is associated with these formations and includes woodland, dry sclerophyll, "mixed forest" (*Eucalyptus*, *Syncarpia*, *Tristania*, dominating a rainforest element stratum) and rainforest. West of Port Macquarie the Carboniferous formation rises to over 4000′. On a part of this area blackbutt forest is developed on greywacke, as is



CLIMATOLOGICAL MAP

(After de Beuzeville, 1943)

INDEX TO CLIMATES BASED ON SWAIN, 1938

KEY TO SYMBOLS:

MTHM = Mean Temp. Hottest Month
MTCM = Mean Temp Coldest Month
MMR = Mean Monthly Rainfall
MAR = Mean Annual Rainfall

SUB-ZONE FACTORS		ZONE FACTORS							
		No. of months MMR falls below 200 points.							
		0 – 1		2 – 4		5 – 7		8 – 12	
MTCM deg F	MTHM deg F	MAR	INDEX	MAR	INDEX	MAR	INDEX	MAR	INDEX
34 to 46	<68	<40 40-60 >60	1.3 a 1 3 b 1 3 c	< 35 35-50 >50	3 3 a 3 3 b 3 3 c	< 25 25-40 >40	5 3 a 5 3 b 5.3 c	< 8 8-15 >15	7 3 a 7 3 b 7.3 c
	>68	<40 40-60 >60	1.4 a b c	< 35 35-50 > 50	3.4 a b c	< 25 25-40 >40	5 4 a b c	< 8 8-15 >15	7 4 a b c
46 to 55	<72	<40 40-60 >60	1.5 a b c	< 35 35-50 > 50	3.5 a b c	< 25 25-40 >40	5 6 a b c	< 8 8-15 >15	7.5 a b c
	>72	<40 40-60 >60	1 6 a b c	< 35 35-50 >50	3 6 a b c	< 25 25-40 >40	5 6 a b c	< 8 8-15 >15	7.5 a b c
55 to 67	<75	<40 40-60 >60	1 7 a b c	< 35 35-50 > 50	3 7 a b c	< 25 25-40 >40	5 7 a b c	< 8 8-15 >15	7.7 a b c
	>75	<40 40-60 60-100	1 8 a b c	< 35 35-50 50-85	3 8 a b c	< 25 25-40 40-60	5 8 a b c	< 8 8-15 15-25	7 8 a b c

Fig. 3. Illustration of principal climatological data in south-eastern Australia. White mahogany, blackbutt and rainforest communities have a common distribution restricted to zones indicated by the initial numeral "1" in the climatic index.

white mahogany forest, Sydney blue gum-brush box forest, and rainforest including Antarctic beech (*Nothofagus moorei*) around 4000′ elevation. It will be demonstrated that variation in greywacke mineralogy may be primarily responsible for some of the vegetation pattern in this area.

Blackbutt has extensive occurrence on coastal deposits of Recent origin, for example Fraser Island, and the Myall Lakes area (Osborn and Robertson, 1939). The association of blackbutt with Recent deposits is restricted to coastal sands; the species rarely occurs on Recent alluvium associated with coastal streams, which frequently carried rainforest.

Rocks of volcanic origin are widespread along the Australian east coast. These range from basic fine-grained basalts to highly acid granites. They vary in occurrence from extensive flows occupying thousands of square miles to localized outcrops of granite interbedded with other strata. Within the Lorne Basin intrusions of both granite and "alkaline intrusive" (dolerite) have uplifted part of the Basin; white mahogany forest occupies the dolerite and blackbutt the granite. In northern New South Wales on Whian Whian State Forest, Baur (1957) has recorded a belt of blackbutt forest on acid rock (rhyolite) "sandwiched" between upper and lower rainforest on basalt, and in southern Queensland the mosaic of blackbutt and white mahogany forest is largely related to the mosaic of rhyolite and trachyte respectively, forming the acid phase of the Triassic "North Arm Volcanics".

Delineation of Rainforest and Eucalypt Sclerophyll.

The most extensive and continuous occurrences of rainforest in New South Wales and southern Queensland are associated with basic volcanic rocks, notably basalts, but only where red loams rather than black earths have developed on them. In a detailed study of lithology in relation to rainforest in southern Queensland, Webb (1956) concluded that subtropical rainforests are not generally supported by sedentary soils from acid rocks, i.e. with silica much in excess of 50%. Where rainforests appeared to be developed on such soils some form of basic enrichment could usually be evidenced. For example, Webb has suggested that polygenetic soils are responsible for rainforest on highly siliceous phyllite. Recent exposure of phyllites by partial erosion of a basalt capping has occurred, but the closed nutrient cycle in rainforest has retarded soil impoverishment even under intense leaching conditions.

The existence of numerous patches of rainforest developed as a function of topography within eucalypt-sclerophyll suggests the possibility that soils formed from some parent materials, though limiting in certain properties for rainforest formation, may be capable of supporting rainforest with colluvial concentration of nutrients or with higher levels of soil moisture. Because of the superimposition of a complexity of such factors on the parent material-vegetation relationship, precise determination of vegetation in relation to lithology will probably not be possible.

Vegetational Delineation in Relation to Parent Rock Mineralogy.

The distribution of blackbutt and white mahogany in relation to the mosaic of geological strata suggested that an examination of the mineralogy of a range of parent materials might reveal some features that would characterize the presence of the respective communities. Micro-sectioning of some 20 rocks was carried out in the Department of Geology, and the results are examined for a number of localities.

1. *Lorne Triassic Basin.* All soils associated with these depositions carry blackbutt, and all have a high quartz content. Conglomerates and coarse-textured sandstones are associated with blackbutt's vegetational gradient towards dry sclerophyll, and depositions with a more complex mineralogical composition with the gradient towards rainforest. For example, a blackbutt-Sydney blue gum-tallowwood forest with some rainforest element is developed on a fine sandstone, with 50% detrital quartz grains, 10% felspar and a considerable amount of epidote.

Within an area of apparently homogeneous rock, contrasts in mineralogical composition may have a considerable influence on the vegetational composition. For example, on a section of the Lorne Basin, the occurrence of a community with blackbutt, flooded gum, brush box and a rich rainforest element stratum might have been assumed to result from topographic influences on the soil derived from the epidote-rich sandstone just described, were it not for puzzling inconsistencies in this pattern. Mineralogical analysis of the apparently similar underlying rock showed that it had no epidote, but had a large amount of clay minerals, particularly chlorite; this parent material difference may well be the primary cause of the vegetational pattern.

Discontinuity of blackbutt within the limits of the Lorne Basin is associated with various exposed Carboniferous strata, and with intrusions of basic plutonic rock. All carry white mahogany. A Carboniferous shale had a small component of very fine quartz (15%), felspar, white mica and abundant muscovite; a fine felspathic sandstone had 10–15% quartz with potash felspar as small grains with a matrix of mica and indeterminate material, and the basic plutonic rock (dolerite) was low in quartz but contained lime-rich felspar, augite, hornblende and magnetite.

2. *Bellangry Forest.* (Carboniferous strata.) Four rocks from contrasted communities were examined. All were greywacke and were indistinguishable on ocular inspection. However, they varied as follows:

(*a*) *Blackbutt forest, little rainforest element*: angular quartz grains 30%, fine grained biotite 30%, remainder fine grained and possibly weathered to kaolin.

(*b*) *Blackbutt, Sydney blue gum and rainforest element understorey*: quartz 10%, biotite 40–50%, small quantity of muscovite, and remainder potash felspar.

(*c*) *Sydney blue gum, brush box, with Argyrodendron rainforest in gully*: biotite 50–60%, and quartz as occasional larger grains forming 5–10% of the total.

(*d*) *White mahogany*: mineralogically distinct from above, particularly low quartz content, and a high component of fine-grained chlorite minerals.

With respect to the first three communities (*a-c*), a vegetational gradient from blackbutt-sclerophyll forest to rainforest is associated with a gradient in the quartz-biotite relationship; a rock relatively high in quartz content supports almost "pure" blackbutt forest, and on the other extreme, a rock relatively high in biotite and low in quartz supports *Argyrodendron* rainforest. It is possible that this quartz-biotite relationship reflects a gradient from acid to basic rock, in which case the vegetational expression would be in agreement with Webb's (1956) conclusions concerning rainforest distribution and the nature of the parent material.

3. *Cooloolabin Forest.* (Acid and intermediate volcanic rocks.) Several rock specimens from each of blackbutt and white mahogany forest respectively were examined.

(*a*) *Blackbutt forest*: (i) *some turpentine component, no brush box*; rhyolite, phenocrysts of quartz in a ground mass of fine potash felspar, and a small percentage of chlorite. (ii) *as* (i); acid rhyolitic lava, large phenocrysts quartz forming a high percentage of total, in fine ground mass felspar and plagioclase. (iii) *high brush box and turpentine component*; altered trachyte, microcrystalline, felspar about 95% of rock, extremely altered, secondary minerals, zeolite and chlorite; quartz veins 5% of rock.

(*b*) *White mahogany forest*: (i) trachyte, quartz nil, dominant minerals potash-felspar and plagioclase. (ii) trachyte, no quartz, texturally different from (i).

Within the acid phase of the North Arm Volcanics of Cooloolabin Forest, there is apparently a gradient in rock mineralogy from the acid rhyolites to the intermediate trachytes. Blackbutt forest that is characteristic of the vegetational gradient towards dry sclerophyll forest is associated with the rhyolites, and all white mahogany forest examined has been developed on trachytes. However, apart from these extremes, there is apparently no precise definition of the forest community in terms of the rock mineralogy; for example, in a more detailed study of the vegetation pattern of Cooloolabin Forest to be presented elsewhere it will be shown that blackbutt and white mahogany forest may occur mosaically on the one parent material.

In summary it is apparent that in many areas the distribution of blackbutt is primarily related to the mineralogy of the parent material. While the mineralogical examinations have been too limited to characterize with any certainty a type of parent material on which blackbutt forest is developed, if indeed this is at all possible, it is clear that in many cases blackbutt is associated with a rock high in quartz content, and absent from fine grained rocks low in quartz, and with high percentages of such minerals as chlorite, mica and magnetite.

In what way the parent material may be primarily responsible for vegetational differentiation is examined in succeeding sections.

IV. The Physical Soil Factor in the Vegetational Pattern.

The role of mineralogical composition of the parent rock in the soil-forming process cannot be defined directly. Under one climatic environment identical soils are commonly derived from contrasted rock types. Nevertheless the mineralogical composition, texture, and hardness of the underlying rock, and its general habit and direction of cleavage are properties which have an important bearing on pedogenesis.

Physical Properties of Blackbutt and White Mahogany Soils.

1. *Rock-Soil Relations*: Through the region studied it is evident that the mineralogy of the parent rock has been a principal controlling factor in the nature of the soil profile formed. Weathering of many rocks with a high or moderate quartz content has been rapid and relatively deep mature soils have formed on them, or alternatively the rock has fractured to depth and an undulating soil/rock boundary formed. In contrast, many of the rocks that have a low quartz content, particularly those with a fine-grained ground-mass of chlorite and mica minerals, have weathered more slowly, producing in many cases immature soils over massive parent rock. On the other hand, deep soils formed on rocks with nil or low quartz carry blackbutt forest, or blackbutt may be developed on parts of the one parent material where formation of deeper soils has occurred, for example, as a function of topography. It is apparent that the nature of the soil profile formed rather than the mineralogy of the rock *per se* is the determining factor in blackbutt–white mahogany differentiation, and that many examples of the correlation between forest community and rock mineralogy can be extended to a correlation between forest community and the nature of the rock-soil relationship. Some examples are given (Table 1).

Generally a striking variation in the rock-soil relationship is associated with a lithological change. However, in a number of instances blackbutt and white mahogany are sharply delineated on the same rock type, and in similar topographic situations, as a result of variation in the structural characteristics of the rock. For example, in Pine Creek State Forest (Table 1) blackbutt occurs where the schist has been tilted to 45° and fractured, facilitating much deeper weathering through moisture infiltration of the laminated rock structure; where the rock is undisturbed and horizontally bedded, and the soil is relatively shallow, white mahogany forest is developed. Again, in Myall River Forest, white mahogany forest occurs on a shallow immature soil overlying massive and very hard dacite. On one part of the forest, blackbutt is found on a deeply weathered soil derived from the same parent material; in this latter case it is possible that the part of the magma had shattered during cooling and deep weathering was facilitated.

2. *Texture and Structure of the Soil*: Although discontinuity of blackbutt and white mahogany can be correlated with the nature of the rock/soil relationship in a large number of cases, there are, alternatively, many examples where variation in the physical properties of the soil itself appears to be a causal factor in the differentiation. For all profiles examined, texture, the nature of soil aggregates and bulk density were recorded. Texture and structure of the soil may affect plant distribution and growth indirectly by their influence on aeration, water movement, water retention and root ramification. For comparable soil textures, bulk density may be regarded as a useful comparative measure of soil aeration and root penetration potential. For example,

Veihmeyer and Hendrickson (1948) suggest that compacted soil layers whose bulk density exceeds 1·75 for sand and from 1·46 to 1·63 for clays may prevent the penetration of roots. In Table 2 a number of examples are given of contrast in the physical properties of profiles carrying sharply delimited blackbutt and white mahogany forest respectively.

From this set of data it seems that blackbutt discontinuity might also be correlated with soils of heavy texture, where soil structure is such that aeration and root ramification might be restricted. Blackbutt is certainly not restricted on heavy textured soil, but may occur only where the soil is well aggregated and bulk densities are moderate.

TABLE 1.

The Rock-Soil Relationship in Adjacent Blackbutt and White Mahogany Forests.

Blackbutt.		White Mahogany.	
(i) Parent Rock. (ii) Soil Group.	Profile.	(i) Parent Rock. (ii) Soil Group.	Profile.
Bateman's Bay.			
(i) Chert. (ii) Podzol.	To 40″ light clay with pieces of quartz and angular chert. Below 40″, chert fragments increasingly compact.	(i) Schist. (ii) Prairie soil.	12″ of light clay with copious parent material fragments over decomposing but compact schist in original laminations.
Manning River (Lorne Basin).			
(i) Fine sandstone. (ii) Krasnozem.	Very deep porous soil.	(i) Shale. (ii) Immature.	Angular shale fragments throughout profile becoming dense and compact at about 15″. At 30″ mainly shale.
Bellangry.			
(i) Greywacke (30% quartz) (ii) Krasnozem.	Deep porous profile; some bands of weathered rock present, but no barrier to moisture on roots.	(i) Greywacke (low quartz–high chlorite). (ii) Immature.	Angular rock fragments and soil of light texture to 15″, below 15″ rock increasingly massive.
Pine Creek.			
(i) Schist. (ii) Yellow podzolic.	Loam and clay loam over shattered schist in parts deeply weathered.	(i) Schist. (ii) Immature.	Variable shallow soil to 24″ over massive horizontally bedded schist.
Cooloolabin.			
(i) Trachyte. (ii) Yellow podzolic.	Grey brown clay loam over a yellow brown clay and heavy clay; deep profile.	(i) Trachyte. (ii) Brown podzolic.	Grey brown loam to 15″, yellow brown clay to 30″, over a massive parent rock.

The evidence presented this far would suggest that the distribution of blackbutt is limited by any physical properties of the soil profile which restrict aeration, moisture permeability or penetration of roots to depth, such soil properties varying with the mineralogy of the parent material, its geological history and the landscape pattern. Blackbutt, however, does not occur on all soils which are apparently adequate in physical properties, and the plant-soil relationships involved in representative cases are discussed later in this paper.

Physical Properties of Rainforest Soils.

Webb (1956) has shown that a suitable range of available moisture and macroporosity are apparently necessary for rainforest formation, but he has stressed that structure in rainforest soils could not be dissociated from the effects of rainforest themselves and so claimed to be causative. Soils which are permeable and well aerated in virgin rainforest may become compacted and waterlogged after removal of the forest, and cultivation. A possible example of the critical nature of soil structure for rainforest formation is seen on soils developed from Carboniferous shale in Coopernook Forest. Normally the moist gully habitats support a typical mixed sclerophyll and rainforest element. The soils are heavy textured and notably subject to waterlogging. However, an isolated patch of rainforest has formed in a small alluvial fan at the base of a gully formed along the junction of the shale and a relatively sterile Triassic sandstone. The presence of the rainforest might be attributed to the simultaneous build up of clay colluvium and sandstone fragments, resulting in the formation of a clay loam with well-developed structure and a particular low bulk density: at 3″, 0·96; at 15″, 0·90; and at 33″, 0·86. In the absence of the ameliorating sandstone influence, the mixed forest may represent an "edaphic climax", restricted by deficiencies in the soil structure.

TABLE 2.

Physical Properties of Soils Associated with adjacent Blackbutt and White Mahogany Forests.

(i) Parent Rock. (ii) Soil Group.	Profile.	Depth.	Density	Notes.
Manning River State Forest.				
(*a*) *Blackbutt.*				
(i) Sandstone. (ii) Krasnozem.	Clay loam over light clay; coarse granular structure.	3″ 18″ 33″	0·80 1·24 1·34	Deep, permeable with good aeration characteristics.
(*b*) *White Mahogany.*				
(i) Felspar-sandstone. (ii) Yellow-red podzolic.	Fine granular sandy loam to 6″ over red and yellow mottled stiff sandy clay, fine blocky structure.	3″ 15″ 33″	1·27 1·44 1·56	Even at the surface B.D. is high, and at 33″ root penetration aeration may be impeded.
Manning River State Forest.				
(*a*) *Blackbutt.*				
(i) Sandstone. (ii) Podzol.	Loan to 10″ where sharp transition to red brown stiff clay, and gradual change to pale grey sandy clay streaked with yellow, red, brown; in B horizon coarse blocky structure.	3″ 15″ 33″	0·93 1·30 1·50	Both of these communities are part of a mosaic on what is a marginal blackbutt site. The white mahogany (*E. umbra*) is present throughout the blackbutt forest but also occurs in depapuerate patches; the very compact clay horizon in these latter situations may be limiting for blackbutt.
(*b*) *White Mahogany.*				
(i) Sandstone. (ii) Podzol.	Sandy loam to 8″ where sharp transition to yellow brown sandy clay changing to heavy clay at 27″, the latter granular and exceptionally compacted.	3″ 15″ 27″	1·27 1·44 1·77	
Queens Lake State Forest.				
(*a*) *Blackbutt.*				
(i) Sandstone. (ii) Yellow-red podzolic.	0–5″ sandy loam, 5–15″ yellow brown light clay. 15–36″ red brown heavy clay, coarse blocky structure breaking to fine blocky.	3″ 15″ 33″	1·19 1·35 1·33	In spite of heavy textured subsoil, the good structural characteristics and moderate bulk density indicate reasonable aeration, moisture and root penetration potential.
(*b*) *White Mahogany.*				
(i) Basic conglomerate. (ii) Podzolic.	Variable depth over rock, but where relatively deep, a granular sandy clay.	3″ 15″ 33″	1·07 1·45 1·62	Combination of rock habit, texture, lack of particle aggregation, and high bulk density would restrict aeration and permeability.

V. SOIL MOISTURE AND THE VEGETATION PATTERN.

Although the many difficulties inherent in an adequate examination of the soil moisture factor in community differentiation were well appreciated, it was felt that a comparative study of soil moisture availability patterns would provide some initial information on forest community–soil moisture relationships that could lead to a later, more critical evaluation of the soil moisture factor in the vegetational mosaic.

During the period April, 1959, to August, 1960, soils were sampled for moisture determination at six-week intervals in three blackbutt, three white mahogany and three rainforest and marginal rainforest communities. In each community samples from three borings were taken at 4″ and 40″; these were dried at 105° C for 48 hours and moisture content expressed as a percentage of oven-dry weight. For each soil and depth, determinations in triplicate were made of Wilting Point and Field Capacity, using pressure membrane apparatus under a tension of 15 atmospheres for five days and ⅓ atmosphere for two days respectively.

Unfortunately for a study of this nature, most of the experimental period was characterized by atypically high rainfall. Normally the months of greatest potential moisture stress are August to November, but in 1959 more than double the mean rainfall was recorded for this period. However, dry conditions prevailed from July, 1960, to October, 1960, with less than one-third normal rainfall, and the pattern of drying for the various soils has been demonstrated.

The pattern of change in soil moisture in relation to Wilting Point and Field Capacity is shown for each of four adjacent communities in Bellangry State Forest (Fig. 4). Three communities are developed on krasnozemic profiles, namely (i) blackbutt with little rainforest element; (ii) Sydney blue gum-brush box-tallowwood, grading downslope into (iii); subsequently referred to as "marginal rainforest"; (iii) rainforest characterized by presence of *Argyrodendron trifoliatum*. The fourth community, white mahogany, is on a brown podzolic.

The blackbutt forest had clearly the most favourable soil moisture characteristics, a wide range of available moisture, and a soil moisture level consistently approaching Field Capacity. In both the rainforest and marginal rainforest soils, ranges of available moisture were comparatively restricted, and at 4″ the soil moisture had fallen below Wilting Point before the final sampling in October, 1960. At 40″ the blackbutt soil was consistently above the Wilting Point until the August, 1960, sampling. In contrast, the marginal rainforest soil was particularly droughty, being above Wilting Point in only three samplings at 40″; inside the rainforest itself, at the base of the slope, soil moisture was more readily available at this depth.

At Coopernook the position was much the same. At 4″ a blackbutt forest soil (a krasnozem) had a wide range of available moisture and a moisture content generally in the upper part of that range. The rainforest soil developed on the alluvial fan (Section IV) was surprisingly droughty, mainly because of the high Wilting Point. At 40″ the rainforest soil fluctuated close to Wilting Point, but the blackbutt soil was consistently above that level. Two white mahogany soils at Coopernook showed rapid soil moisture fluctuation at 4″, but at 40″ soil moisture was much more stable.

One of the striking features of the data obtained is that unless rainforest species which draw their moisture supply principally from the 0–40″ depth range are able to obtain moisture at levels below the permanent wilting percentage, then these species must be subject to moisture stress in most years and severe moisture stress in periodic drought years.

The comparative status of soil moisture availability in the eucalypt-sclerophyll and gully rainforest is surprising. Undoubtedly it may be related in part to the greater moisture usage under rainforest, but in addition the question arises as to whether rainforest, by virtue of its own effect on soil pore characteristics (through the nature of its litter and organic matter), effectively limits the availability of soil moisture to itself. This is suggested by the range in available moisture for four krasnozem profiles, as follows.

	Field Capacity. (% Soil Moisture.)	Permanent Wilting Percentage. (% Soil Moisture.)	Range of Available Moisture.
Blackbutt Forest, Coopernook	54	27	27
Blackbutt Forest, Bellangry	50	24	26
Marginal Rainforest, Bellangry	49	32	17
Rainforest, Bellangry	57	41	16

Webb (1956) has also commented on the narrow range of available moisture found in many rainforest soils; he found there was a high percentage of small pores in the soil and Wilting Points were typically high. For this reason, he stated, rainforest required climates which were relatively moist during the year. It seems, therefore,

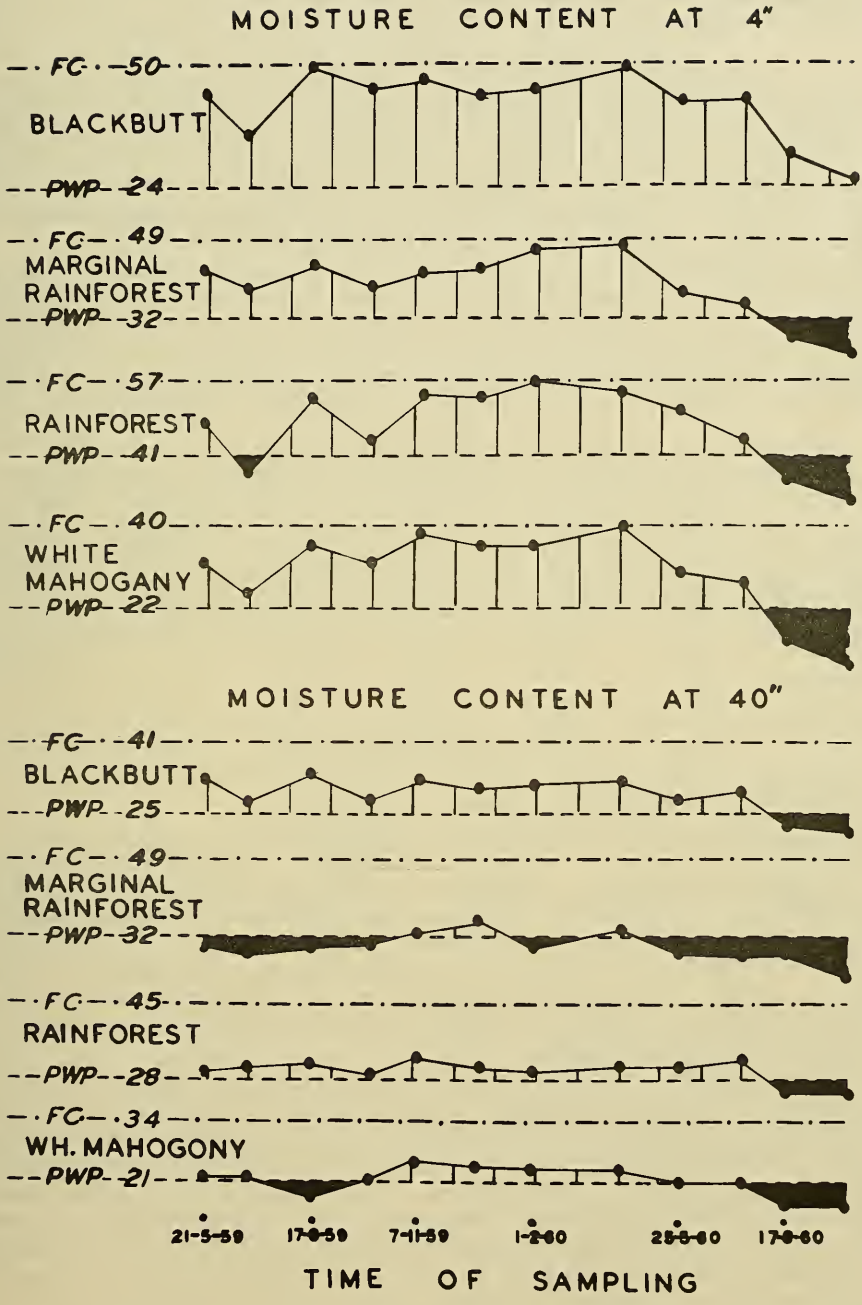


Fig. 4. Patterns of change in soil moisture at 4″ and 40″ in four forest communities at Bellangry. Soil moisture content was expressed as a percentage of oven-dry weight, and for each community has been plotted between the soil's Field Capacity (FC) and the Permanent Wilting Percentage (PWP). Vertically hatched and darkened sections illustrate available moisture and possible soil drought respectively.

that under conditions where other soil properties are not limiting for rainforest, soil moisture availability would be a critical factor in its distribution. At lower elevation, or in steep topography, rainforest might be restricted to gully habitats, but if the same soil were at higher elevations, or in more gently underlying relief, rainforest could be the dominant vegetation.

VI. The Nutrient Factor in the Vegetation Pattern.

The total amount of nutrient available to a plant in a given soil is primarily a function of the lithology of the parent material and the weathering to which it has been subjected. It is also a function of the vegetation present through its effect on (i) differential use or accumulation of various elements, (ii) distribution of total nutrients through the soil-plant ecosystem, (iii) rate of nutrient mineralization from the organic matter, and (iv) the nature of plant-microbiological interactions.

It is apparent then that in ecological studies the use of the pot-nutrient technique for determination of the soil-nutrient factor in plant distribution may have certain limitations. This was well illustrated in this study. It had been planned to examine the possibility that a soil-nutrient factor might be responsible for the ecological differentiation of blackbutt and white mahogany by nutrient studies with blackbutt seedlings in a number of white mahogany soils, and with white mahogany seedlings in a number of blackbutt soils. Following the demonstration of the severe inhibition of blackbutt and other plants in a blackbutt soil (Florence and Crocker, 1962) this approach seemed hardly justified. However, blackbutt seedlings did not develop symptoms of inhibition in *E. acmenioides* soil, and the use of the pot-nutrient technique has made possible some conclusions concerning (i) the nutrient status of white mahogany soils for growth of blackbutt and (ii) relative fertility status of *E. acmenioides* and *E. umbra* soils.

Table 3.

Yield of Blackbutt in White Mahogany Soils. Mean Leaf Area Production per Pot—Sq. Inches.

	No Addition.	Minus[1] P.	Minus N.	Minus K.	Minus Ca.	Minus Tr.[2]	Complete Nutrient.
E. acmenioides Soil (I).	64·2**	99·2*	75·1**	118·4	118·8	117·5	117·5
E. acmenioides Soil (II).	78·7**	86·9**	115·7**	140·0	141·1	—	143·1
E. umbra Soil (III).	9·3**	14·3**	46·4**	80·1**	82·4**	91·7	89·7
E. umbra Soil (IV).	39·8**	79·1	52·9**	91·6	88·9	—	90·0

[1] Complete nutrient addition minus P . . . (etc.).

[2] Trace elements.

For each soil, differences from " complete nutrient ". * Significant at 5% level ; ** significant at 1% level.

Soils were sampled from the surface 6″ in two *E. acmenioides* forests and two *E. umbra* forests; they were coarse-sieved, and for each soil equal amounts by weight were placed in 8″ diameter pots. The "omission method" for exploratory examination of nutrient deficiencies was used in each case, and the "complete nutrient addition" consisted of NaH_2PO_4 at 4 cwt/acre, NH_4NO_3 at 1 cwt/ acre, KCl at 1 cwt/acre, CaCO at 2 cwt/acre, $MgSO_4$ at 1 cwt/acre, and a mixed trace element solution containing Fe, Bo, Mn, Zn, Cu and Mo. All nutrients except Ca were added in solution. Summarized yields (leaf area production per pot) are presented in Table 3.

Although lower yields were obtained in the absence of either N or P in *E. acmenioides* soils, blockbutt seedlings developed well without nutrient addition. In *E. acmenioides* soil No. I, the main response was to N with a smaller response to P. In this same soil under field conditions excellent growth of cotyledonary transplants was obtained, though seedlings were a pale green throughout. In *E. acmenioides* soil

No. II all seedlings were a dark healthy green including those without nutrient addition, but nevertheless a response to both N and P was obtained. In view of blackbutt's response to N and P on a high site quality blackbutt soil, especially after air-dry storage or mild heat treatment (Florence and Crocker, 1962), there seems little basis for suggesting that responses to these nutrients in this case indicate a critical deficiency in the soil limiting blackbutt's occurrence on the soil.

The yield pattern on *E. umbra* soils suggests the possibility that N and P deficiencies could be limiting for blackbutt. The failure of seedlings on the unaltered *E. umbra* soil No. III might not be attributed to microbiological inhibition, as the seedlings exhibited neither leaf purpling nor severely restricted root development. *E. umbra* soil No. IV was obtained from a depauperate community marginal to blackbutt forest on sandstone (Table 2). The soil was a pale sand, and in view of the nature of the vegetation, some marked deficiencies were expected. However, absence of added P had no, or possibly a very slight effect on yield, but absence of added N had a depressive effect. Even with complete nutrient leaves were slightly chlorotic, and it appears that level of N added was inadequate, particularly in the presence of added P.

From the lithological, soil profile and nutrient study, some tentative conclusions concerning differentiation of blackbutt and white mahogany are now possible.

(i) Blackbutt is not necessarily restricted by a soil nutrient deficiency from *E. acmenioides* sites, a conclusion supported both by glasshouse and field studies.

(ii) The relationship between blackbutt nutrient requirement and *E. umbra* soils is not clear. Their frequent co-occurrence indicates a considerable overlap in their physiological tolerances. The adequate soil P in the depauperate *E. umbra* community (Soil No. IV) suggests a blackbutt tolerance of soils of particularly low fertility status.

(iii) By and large, therefore, it seems that the delimitation of these interbreeding species is related to the physical characteristics of the soil rather than to its nutritional status.

TABLE 4.

Exchangeable Cations and Phosphorus in Soils from a Range of Vegetational Types.
(From Baur, 1957.)

	Exch. Cations. (m.eq/100 gr.)	Exch Ca.	Exch. K.	Total PO_4 p.p.m.
Rainforests with *Argyrodendron* ..	15·8–62·0	10·5–47·2	0·8–2·8	2940–7620
Rainforests with *Ceratopetalum* ..	2·3–11·3	1·1– 3·5	0·6–1·0	520–1090
Wet sclerophyll	6·8–10·2	2·3– 5·9	0·5–0·7	480–1710
Dry sclerophyll	0·9– 4·5	0·4– 3·2	0·1–0·9	110– 226

The Nutrient Factor in the Vegetational Gradient to Rainforest.

Within both blackbutt and white mahogany communities, the largely parallel gradients from xeromorphic to mesomorphic vegetation (Florence, 1963) are undoubtedly associated with gradients in soil fertility status. In agricultural development in eastern Australia, the rainforest areas of reasonable relief were the first to be settled, although subsequent deterioration in nutrient status of many of these soils has been rapid. The association of rainforest with basic parent materials, or with soils enriched with basic materials, points to a high fertility requirement, and in fact Beadle (1954, 1962) has shown that an increase in phosphorus content of parent materials and soils in the Sydney district is associated with vegetational gradient from dry sclerophyll to rainforest. Data presented by Baur (1957) show that soils of the most highly developed rainforest type in New South Wales (characterized by the presence of *Argyrodendron* sp.) are particularly high in exchangeable cations and phosphorus (Table 4). On the other hand Baur's data show that certain "wet-sclerophyll" communities, and rainforest communities characterized by the presence of *Ceratopetalum*, are associated with much the same range of values for soil phosphorus and exchangeable cations. While this suggests that *Ceratopetalum* and *Argyrodendron* rainforests may be delineated by soil fertility status, studies of the total nutrient content within the "wet sclerophyll" and *Ceratopetalum* rainforest ecosystems would be necessary to determine their nutrient relationships. Rainforests may have much greater amounts of nutrients immobilized in the dense crown layers, and these are probably circulated through the plant-root system at a much faster rate than in eucalypt forests. It may be that "wet-sclerophyll" forests with soil nutrients at the upper limit of the given range may be limiting in soil moisture for *Ceratopetalum* rainforest development and, alternatively, *Ceratopetalum* rainforest soils with nutrients at the lower limit of the given range may have a very favourable and compensating soil moisture regime. Alternatively some superimposed factor such as the fire history of the forest could tip the balance between sclerophyll forest near the upper limit of the vegetation gradient towards rainforest, and *Ceratopetalum* rainforest.

VII. The Community-Site Interaction as a Factor in the Vegetation Pattern.

Florence and Crocker (1962) have suggested that the nature of the interaction of a plant community with its environment can be a critical factor in determination of vegetational relationships. This was based on their investigations into the severe inhibition of blackbutt seedling growth in blackbutt forest soil, and the finding that some component of the soil microflora was directly antagonistic to blackbutt seedling roots. A tentative hypothesis suggested that the development of a blackbutt forest might depend on a considerable degree of fluctuation in the microbiological environment and that, along gradients of decreasing potential for that fluctuation, the interaction of blackbutt with its site would be increasingly adverse, resulting in modification to the blackbutt community, and eventually to its complete replacement.

The possible application of such an hypothesis to explain some otherwise puzzling aspects of blackbutt's vegetational relationships is examined for two typical situations.

(i) *Possible Mechanism Restricting Blackbutt along a Gradient of Increasing Permanence in Soil Moisture Status.*

A widespread vegetational pattern on Silurian schists and shales of the Coffs Harbour area is the occurrence of blackbutt forest on ridges, with rainforest in gullies and with a variable strip of white mahogany forest interposed between the two. Soil profiles were examined along several road cuttings in Newry and Orara Forests, but no marked differences in physical properties were found. It was noted, however, that the soil exposed in cuttings on lower slopes (carrying white mahogany forest) was apparently moister than on upper sections of the slopes (carrying blackbutt forest). This probably resulted from the tilt and low permeability of the schist rock with consequent movement of moisture downslope rather than to depth. If the development of a blackbutt forest, on some soils at least, is partly dependent on fluctuation in the microbiological environment as hypothesized, then this may be achieved to a large degree through fluctuation in soil moisture and through the resultant cumulative effect of the drying and wetting cycles on stimulation of microbiological activity and organic carbon and nutrient mineralization (Birch, 1958). Under conditions where level of soil moisture may be relatively stabilized by slow moisture infiltration, the microbiological condition created through incorporation of blackbutt litter could well interact adversely against this species, and an alternative species so enabled to gain dominance. In this respect it is possibly significant that the properties of *E. acmenioides* litter are such that no apparent inhibition was found in several *E. acmenioides* soils.

(ii) *Possible Mechanism Restricting Blackbutt along a Gradient of Increasing Soil Fertility.*

On part of Bellangry Forest a quite striking vegetational pattern consists of an alternating occurrence of sharply delimited blackbutt and marginal rainforest communities (Sydney blue gum, brush box, tallowwood). Both extend from ridge to gully habitats, the former having little rainforest element and the latter a low rainforest element on slopes and *Argyrodendron* rainforest in a broad fan at the base of the slope.

These contrasted communities are both developed on krasnozem profiles similar in general appearance; both have clearly had a history of fairly severe fires before protection. What then is the reason for their sharp delimitation?

The blackbutt forest soil is associated with a parent material with a higher quartz and lower biotite content than the marginal rainforest soil (Section III). Both the blackbutt parent material and soil are more weathered, the blackbutt soil being a clay and the marginal rainforest soil a loam. In view of the variation in rock mineralogy, the weathering status of rock and soil, and the lower slope occurrence of *Argyrodendron* rainforest on the marginal rainforest soil, it can be indirectly inferred that this latter soil has a considerably higher fertility status. The question becomes one of suggesting how a soil that is probably not limiting in other directions can, by virtue of a high fertility status, sharply restrict the presence of blackbutt. Both of these soils were shown to inhibit severely blackbutt seedling development (Florence and Crocker, 1962), but seedlings in the marginal rainforest soil were strikingly chlorotic in contrast to the typical purpling of inhibited seedlings in a blackbutt forest soil. Although blackbutt seedling growth is restricted in an undisturbed blackbutt forest soil, it is possible that blackbutt seedlings could be even more sensitive to the various influences of certain other species on soils of high fertility status, and in this way there could be an effective barrier to blackbutt seedling establishment and survival on those soils.

In the example described, the blackbutt forest was sharply delimited from the marginal rainforest along an edaphic boundary. But frequently the same accumulation of dominants (Sydney blue gum, tallowwood, brush box) dominating a rainforest element stratum is interposed between blackbutt forest and rainforest along a uniform environmental gradient. In such cases an increasing fertility status through colluvial enrichment, or increasing permanence in soil moisture status, or both, may well create conditions with which blackbutt would interact unfavourably, and so result in a gradual displacement of blackbutt from the community.

DISCUSSION.

The main conclusions from the study of edaphic relationships in east coast vegetation can be summarized as follows:

(i) The interbreeding species blackbutt and white mahogany occupy largely distinctive habitats, characterized by differences in physical properties of soils and expressed through variation in potential for soil aeration and root penetration to depth.

(ii) Blackbutt and white mahogany communities occupy largely parallel gradients from open sclerophyllous conditions to mixed sclerophyll-rainforest, and rainforest, respectively. Vegetation gradients may be correlated with gradients of increasing soil fertility status, or to some extent with gradients of increasing soil moisture. Where soil nutrients are particularly limiting, improvement in soil moisture may have little or no effect on the vegetation, and alternatively, where soil nutrient status is high the vegetational gradient may be restricted through soil moisture deficiencies. Irrespective of nutrient or moisture status, vegetation gradients to rainforest may be restricted by limiting physical soil conditions.

(iii) The upper limit of blackbutt's environmental tolerance along gradients of increasing soil fertility, soil moisture, or both, may be determined in part by the nature of its own interaction with its environment. On the other hand, white mahogany may extend along environmental gradients and be marginal to rainforest.

The relationship between the broader edaphic criteria and vegetation can be expressed diagrammatically by illustrating the alignment of vegetation along gradients in physical and chemical soil properties (Fig. 5). The model assumes a geographic location in the centre of the common blackbutt–white mahogany–rainforest range, a low elevation with rainfall around 60″ per annum and a flat topography. The influence of slope on vegetation would vary from point to point on the model, and a key is included showing slope effects for a number of representative situations.

In the foregoing an attempt has been made to show how the complexities of the vegetational pattern in east coast forests composed of blackbutt, white mahogany and rainforest communities may be closely related to variation in physical, chemical and biological properties of the soil. This, however, is probably not a static relationship, even over the geographic range common to all three species; it has been suggested, for example, that brush box and turpentine may have a wider edaphic tolerance in southern Queensland than along the central coast of New South Wales (Florence, 1963). That the relationship between the nature of the vegetation and the parent material and soil does alter is evident from the occurrence of rainforests in North Queensland on soils derived from some types of parent material from which they would certainly be absent in the south.

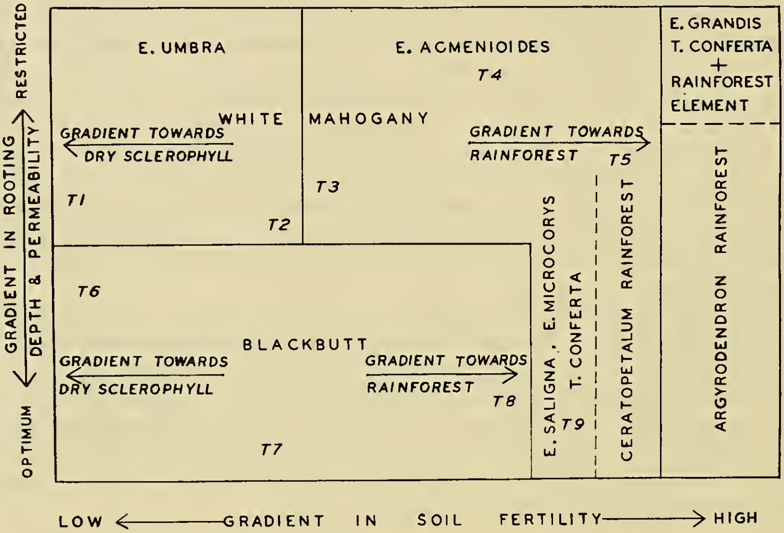


Fig. 5. Diagrammatic illustration of the relationships between vegetation and the broader edaphic criteria. The model assumes low elevation with rainfall around 60″ per annum and a flat topography.

Key to the influence of slope on vegetation at a number of points (T_1, T_2 . . . T_9) follows:

T_1 No changes in dominant strata, slight changes in understorey.

T_2 Some *E. grandis* in broader colluvial situations with a limited shrubby mesophytic element understorey.

T_3 Mixed forest (with *T. conferta*) or *Ceratopetalum* type rainforest.

T_4 Where colluvial material is of good structure—rainforest, but otherwise mixed forest—i.e. *E. grandis,* and *T. conferta* emergent over rainforest.

T_5 Through increasing *T. conferta* to highly developed *Argyrodendron* rainforest.

T_6 On gentler slopes *E. pilularis* decreases and *E. resinifera* and *E. umbra* increase, with some development of mesophytic shrubs. In deeper alluvial situations, a *T. conferta-E. grandis* mixed forest.

T_7 Steep topography is unlikely on this soil. On moderate slopes, scattered mesophytic shrubs develop with some *E. grandis* and *Acmena* and *Eugenia* species along watercourses.

T_8 On slopes, *E. pilularis* decreases and *E. microcorys* and *E. saligna* increase; composition of understorey becomes richer in rainforest element species. On long slopes, *E. pilularis* may cut out, and a *E. saligna - E. microcorys - T. conferta* community may be interposed between the blackbutt and pure rainforest.

T_9 *Argyrodendron* or *Ceratopetalum* rainforest.

Although the actual pattern in Nature may be very complex (Fig. 1), particularly where there is variability in the parent material and where the topography is steep and uneven, it is apparent that the total plant community in a given ecological niche can be regarded as a single unit that is the resultant expression of a number of environmental pressures; and, further, the total community changes sensitively and predictably with changes in edaphic environment. In an earlier paper (Florence,

1963) the concept was advanced that the eucalypt-rainforest relationship can be characterized as a continuum; in terms of environment this concept envisages a gradual change in the composition of both the dominants and the associated rainforest element species along gradients of increasing soil fertility and/or permanence in soil moisture status. In the virgin forests before the advent of man, the expression of the continuum may have been restricted, possibly because of the nature of the eucalypt influence on its own site, and certainly by the superimposed influence of periodic wildfires, resulting in sharp discontinuities in the eucalypt-sclerophyll relationship. Consequent to the advent of man, widespread habitat disturbance followed by complete protection may have led to the so-called rainforest "advance", but this may represent a more complete expression of the continuum through less restricted development of species according to their respective amplitudes.

The concept that the vegetation in a given ecological niche is the sensitive expression of largely the edaphic environment, conflicts with the widely held view that fire incidence is the major factor determining the vegetation pattern, a view summarized by Cremer (1960) in these terms: ". . . From the point of view of the rainforest the eucalypts are but a transient fire weed . . . the mixed forest is then a fire sere in the succession towards the rainforest climax." While it is well recognized that eucalypts, and such other species as turpentine and brush box, will not regenerate within a well-developed rainforest element understorey, it is, on the other hand, open to serious doubt whether the factors of the environment would be adequate to enable a rapid and widespread development of a self-perpetuating rainforest following senescence and death of the dominant stratum in much of the "mixed" forest in eastern Australia. Perhaps at an advanced stage along the environmental and vegetational gradient towards rainforest, the rainforest element stratum could maintain itself as such (e.g., a coachwood community understorey to tallowwood and brush box), but it seems inconceivable that even the most highly developed rainforest element stratum under blackbutt, for example, could maintain itself indefinitely if, as postulated, that element is by necessity composed of species with less demanding edaphic requirements. Although it is accepted that perpetuation of most "mixed" forests may in fact have resulted directly from periodic wildfires or other major disturbances (e.g., cyclones), it is nevertheless suggested that a rainforest-element stratum which is not capable of self-perpetuation following senescence of the dominants would itself decline in time, leading directly to regeneration of the dominants, or creating the vegetational condition conducive to its own destruction by fire.

Ultimately, a real understanding of the complexities of the eucalypt-rainforest relationship must depend on a much more intimate understanding of the various ecosystems, e.g., the total nutrient store, its distribution and re-circulation, the moisture balance, the influence of species and species mixtures on the physical, chemical and biological properties of the soil, and their contribution to the overall biological system. Again, it seems necessary that ecological thought must be directed to the principles contained within Watt's (1947) classic perspective on the dynamics of the plant community. Watt demonstrated, for a wide range of communities, that many dynamic situations may be cyclic, and not, as would appear at a point in time, seral; a species or group of species in a community may undergo a regular series of upgrade and downgrade phases in which there is a continual change in ecological structure. If, in east coast forests, a community of sclerophyllous dominants and rainforest element species form a vegetational unit sensitively in equilibrium with the environment, then in terms of Watt's concept, a downgrade phase (or senescence) of overmature sclerophyll dominants could be associated with an upgrade phase of the rainforest element and, in time, the downgrade phase of the rainforest element with an upgrade phase of the sclerophyll. Long-term analysis of vegetational dynamics in these mixed communities would be necessary to substantiate or reject such an hypothesis, an analysis that would be complicated by the impact of broader (e.g., macroclimatic) changes on the habit-sensitive communities.

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